

Vol. 117. Pt. 12. Pp. 345-365.

31st December 1965

TRANSACTIONS
OF THE
ROYAL ENTOMOLOGICAL SOCIETY
OF LONDON

World List abbreviation : Trans. R. ent. Soc. Lond.

ROBERT W. TAYLOR

A monographic revision of the rare tropicopolitan ant genus
Probolomyrmex Mayr (Hymenoptera : Formicidae)

PUBLISHED BY THE SOCIETY
41 QUEEN'S GATE, LONDON S.W.7.

Price 12s 0d

**A monographic revision of the rare tropicopolitan
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(Hymenoptera: Formicidae)**

By ROBERT W. TAYLOR

Biological Laboratories, Harvard University, Cambridge, Massachusetts, U.S.A.

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With 35 Text-figures

SYNOPSIS

Workers and queens of the genus *Probolomyrmex* are redescribed, and the male and immature stages are described for the first time. Accounts are given of the synonymy, systematic position, life history and biology of the genus. A key to the nine species of the world fauna is included. Descriptions are given of the worker of a new species from Guinea, of the worker of a new species from Guadalcanal and of the worker, queen and male of a new species from Australia. Redescriptions, distribution records and biological notes are given for the remaining six species.

I. INTRODUCTION

THE genus *Probolomyrmex* includes nine known species, three of which are described below as new. Its members have an exceptionally uniform general habitus and are among the most peculiar and easily recognised of all ponerine ants. The group is circumtropical in distribution, with three species in each of the major tropical areas of the globe: African, Indo-Australian and American. These ants are extremely rare; only 57 specimens have been collected, more than half of them in a single sample. Only four species have been taken more than once, none of them more than twice, and only three of them at more than one locality. Three species are represented exclusively by their holotypes, a lone male is known, and the immature stages are available for only one species.

Previous publications on the genus have consisted mainly of scattered descriptions of single species and catalogue lists. No earlier author was able to consider more than a single caste of the species before him, and all previously studied specimens were either workers or dealate queens. A male specimen, described as *Probolomyrmex palauensis* by M. R. Smith, was erroneously associated with the genus and is transferred below to *Leptanilla*. Almost all earlier type material has been gathered for

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consideration in this revision, which attempts to provide a definitive statement of the known taxonomic and biological facts concerning this peculiar and interesting genus.

II. Genus *Probolomyrmex* Mayr

Probolomyrmex Mayr, 1901, *Ann. naturh. Hofmus. Wien* 16 : 2-3. Type species: *Probolomyrmex filiformis* Mayr, 1901, *i.c.* 3, ♀. Type locality: Port Elizabeth, South Africa. Monobasic.
Escherichia Forel, 1910, *Zool. Jahrb. Syst.* 29 : 245-6. Type species: *Escherichia brevisrostris* Forel, 1910, *i.c.*, pp. 246-7, ♀. Type locality: Ghinda, Ethiopia. Monobasic. *syn. n.*

(1) *Synonymy*

As predicted by W. L. Brown (1952), study of the holotype of *Escherichia brevisrostris* shows it to be unquestionably referable to *Probolomyrmex*, thus establishing the above synonymy. Moreover, *brevisrostris* is almost certainly a senior synonym of the Ugandan *P. parvus* Weber (*see* p. 355). The single known *brevisrostris* worker is a perfectly typical *Probolomyrmex*, except for its well developed compound eyes. Separate generic status on the basis of this character would be completely unjustified.

(2) *Characters of the genus*

Worker

Known for all species except the South American *P. boliviensis* Mann.

Small sized monomorphic ponerine ants. Head longer than broad, its maximum width less than 0.5 mm. Clypeus and anterior part of frons produced forwards as a narrow subrectangular shelf bearing the exposed and closely approximated antennal insertions, which are separated by a thin, vertical lamella formed by fusion of the frontal carinae. Mandibles small, elongate-triangular, obscured in facial view by frontoclypeal process; each with an acute apical tooth followed by a series of small denticles, the anterior one of which may be enlarged. Labrum transverse, its anterior border with a deep median cleft. Palpal formula, maxillary 4: labial 2. The 3 basal maxillary palpomeres about subequal in size (1-1.5 times longer than broad), the apical one longer (3-5 times longer than broad). Labial palpomeres subequal in length, about 2.5-4 times longer than broad. Eyes lacking, except in the unique holotype of *P. brevisrostris* (Forel), in which they are well developed, with about 14 facets. Antennae 12-segmented; apical portion of scape with the flexor surface more or less concave in cross-section, receiving the folded funiculus; the latter slightly incrassate but without a distinct segmental club, its second joint sometimes strongly transverse, apical joint about as long as the 3 preceding together.

Body and legs slender. Mesosomal¹ sutures virtually lacking, represented only by weak ventro-lateral traces, as shown in the accompanying figures. Propleura inflated, projecting ventrally. All tibiae with a single pectinate spur; pretarsal claws simple, lacking a median tooth. Declivitous face of propodeum margined on each side by a low obtuse carina, which is usually bluntly dentate above. Petiolar node narrow, strongly arched above, higher behind than in front, with an evenly curved anterodorsal profile and an almost vertical posterior face. The latter usually quite strongly concave in side view and enclosed laterally and dorsally by a low carina. A moderate constriction between first and second post-petiolar segments. Second post-petiolar segment (abdominal IV) with its tergite and sternite fused laterally to form a tubular structure (as usual in ponerine ants). Sting well developed.

Sculpturation with 2 basic components: dense fine shagreening and associated large scattered punctures, latter often weakly incised and rarely lacking. Pilosity very reduced, limited to a few minute bristles on underside of frontoclypeal shelf, some long stout hairs on mandibles and a few fine ones about openings of metapleural glands. Pubescence very fine and short, essentially absent in some species, moderately abundant in others. Colour pale yellowish- or reddish-brown.

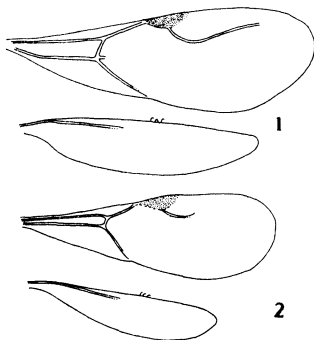
Because of the extreme structural reduction of *Probolomyrmex*, taxonomic discrimination of the species is almost entirely dependent on characters of dimensions and proportions, especially those of the head, antennae and node, and sculptural details.

¹ The term "mesosoma" is here used for thorax + propodeum (*see* Michener, C. D., 1944, Comparative external morphology, phylogeny and a classification of the bees (Hymenoptera). *Bull. Amer. Mus. nat. Hist.* 82: 167).

Queen

This caste is known for only four *Probolomyrmex* species: *parvus*, *greavesi* sp. n., *angusticeps* M. R. Smith and *boliviensis*; all are figured below. The general habitus is very standard, with interspecific differences parallel to those of the workers, which are known for all these species except *boliviensis*.

Size about as in conspecific workers. Structure and proportions of head capsule, frontoclypeal process, mandibles, labrum, labio-maxillary complex, oral palpi, antennae, legs, petiole and gaster almost exactly as in workers; the scapes proportionately a little shorter and the gaster slightly more voluminous. Compound eyes and ocelli well developed. Mesosoma structurally unreduced. Pronotum large; propleura as in worker. Mesoscutum lacking notauli; parapsidal lines fine but distinct. Profile of mesonotum not indented at trans-scutal suture, which is finely incised. Scutellum



FIGS. 1-2.—*Probolomyrmex* Mayr, wing venation: (1) *P. angusticeps* M. R. Smith, queen; (2) *P. greavesi* sp. n., queen.

shield-shaped, its anterior border straight, dorsal outline (viewed from side) evenly convex. Metanotum moderately convex, not produced into a point like that of the male. Saturation lacking between metepisternum and propodeum; general form of latter as in worker.

Wings (known for two species only) long and narrow, with very reduced venation (figs. 1 and 2). Fore wing with a single closed (median) cell. Hind wing with a single longitudinal vein (probably radius + subcosta) and 3 subapical hamuli and with no trace of an anal lobe. Pilosity, pubescence, sculpturation and colour as in conspecific workers.

Male

The only known male of *Probolomyrmex* is a paratype of the Australian *P. greavesi*, which is described below.

General features as in figures 26 and 27. Head subglobose, frontoclypeal region and frontal carinae produced anteriorly as in the female castes. Antennae 13-segmented; scapes relatively long, reaching back to the anterior ocellus; funiculus slightly incrassate, proportions of its segments as shown in figure 26. Mandibles large, triangular, with a single strong apical tooth; masticatory border rounding evenly into posterior one. Palpal formula, maxillary 4; labial 2; proportions of palpomeres as in worker.

Pronotum well developed. Mesonotum lacking notauli; parapsidal lines distinct. Scutellum moderately convex. Metanotum produced into an obtusely pointed median dorsal tooth. Metepisternum separated from propodeum by a strong suture, and itself divided obliquely into anepisternal

vestiges. Mid-ventral prothoracic tubercles displaced laterally by the leg vestiges and a large median welt, which lies across anteroventral part of segment and is apparently not homologous with the tubercles. Each tubercle bears a single median nipple-like papilla, except the prothoracic ventrolaterals, which each carry 2 papillae, the anterior one with a pair of minute bristle-like sensilla. Tubercles and papillae vary in size and shape, as shown in the figures. Integument, apart from the surfaces of the tubercles, densely papilligerous; papillae 0.003–0.005 mm. high, arranged generally in transverse rows. Pilosity completely lacking.

Cranium large, subcircular in anterior view, slightly concave behind. Head naked, except for a few sensilla and some minute hairs. Antennae a pair of low flat subcircular elevations, each with 3 sensilla. Mouthparts only moderately prominent. Labrum small, semicircular, breadth at base slightly more than twice length; apical border entire, with a few small sensilla; posterior surface densely spinulose, the spinules arranged in arcuate rows. Mandibles long, narrow, moderately sclerotised, not greatly expanded at base; apex slightly curved posteriorly and drawn into a strong mesally inclined tooth, with 2 much smaller teeth on its inner border. Maxillae hemispherical. Palpi not peg-like, each represented by a group of 3 sensilla shaped as shown in figure 6. Galea closely adjacent to palpal sensilla, a relatively very small finger-like structure with a slender apical process. Labrum prominent. Palpi reduced similarly to those of maxillae, each represented by a group of 4 sensilla, shaped as shown in figure 7. Opening of sericteria small, slit-like. Hypopharynx spinulose, the spinules arranged in many short arcuate rows.

The *Probolomyrmex* larva is distinguished from those of all other known ponerine ants by the shape of the body and the unique posterodorsal suspensory organ, which is analogous (but clearly not homologous) with the dorsal "doorknob" tubercles found in some genera of the tribe Ponerini (see G. C. and J. Wheeler, 1952, 1964).

Pupa

This stage is known only for *P. angusticeps*, the pupae of which are unusual in that they lack cocoons. A very few other ponerine ants, including some species of *Amblyopone*, *Discothyrea* and *Ponera*, share this same negative characteristic. It is not a universal character in any of these genera and may not be in *Probolomyrmex*.

(3) Life History and Biology

Very little is known concerning the biology of *Probolomyrmex*. The few available ecological details indicate that most of the extra-Australian collections were made in rain-forest, or in islands of native forest in plantations. Nests in such situations are apparently located in leafmould or fragments of rotting wood on the forest floor. A shift in ecological preferences may have taken place in the evolution of the Australian *P. greavesi*; both collections of this species were made in drier forest types (open *Eucalyptus* woodland and an exotic *Pinus* plantation), in which the nests were located in the soil under rocks.

Some features of the social biology of *P. angusticeps* are described below (see page 360). These are based on the only known observations of a live colony of *Probolomyrmex*; unfortunately it is impossible to estimate whether certain features, particularly the peculiar aspects of larval and pupal life and such details as colony size and composition, are normal for the genus. Direct positive feeding records are not available, although the holotype worker of *P. brevisrostris* was taken in a termite nest, where it may have been seeking prey. It is noteworthy that several other ponerine genera (*Discothyrea* and *Proceratium*), which have similar oral and anterior head structure to that of *Probolomyrmex*, are evidently obligatory arthropod egg predators (Brown, 1957). All known sexual forms of *Probolomyrmex* are of the normal winged type, so that colony proliferation probably includes a mating flight, as is usual in ants.

(4) Systematic Position of the Genus

Until recently *Probolomyrmex* was affiliated with *Proceratium*, *Discothyrea*, and other genera synonymous with them, in the spurious tribe Proceratiini Emery. This group was disbanded by Brown (1952, 1958), who showed that the "proceratine habitus" of its included genera has evidently been convergently derived in several

unrelated stocks. *Proceratium* and *Discothyrea* should apparently be included in the tribe Ectatommini, and *Probolomyrmex* appears to be related to *Platythreia* and *Eubothroponera*, constituting with them the tribe Platythreini. The close similarity between *Probolomyrmex* and some *Discothyrea* species, in frontoclypeal structure and other characters, is explained in these arguments as being due to convergent resemblance.

Brown's platythyreine assignment was based on a comparison of *Probolomyrmex* with *Platythreia*, in which characters of habitus and the details of pilosity and sculpturation were considered. He concluded that "the point-by-point agreement is so close that I must consider *Probolomyrmex* to represent a direct derivative of *Platythreia* modified for a highly cryptobiotic existence".

The present paper contains much new information, including details of palpal formulae, wing venation, and male and larval characters. Unfortunately these facts shed little further light on the possible affinities of *Probolomyrmex*; they neither strengthen the argument for a platythyreine placement, nor do they imply a better alternative assignment.

Although the additional female characters of palpal formula and wing venation and structure assist in the taxonomic diagnosis of the genus, they have little value as phylogenetic indicators. The 4 : 3 palpal formula probably also occurs in *Platythreia* (counts of 6 : 4, 3 : 2 and possibly 2 : 2 were given by Brown (1952)), but this formula is also produced in other lines of ant evolution. The wing venation is exceptional in its extreme reduction, to a point where all trace of affinities is lost.

The *Probolomyrmex* male has a decidedly "proceratiine habitus", with the frontoclypeal process at least as well developed as that of any known *Discothyrea* male. Other apparently correlated features include the mandibular structure, the relatively large ocelli and the elongated antennal scapes. Considerable variation is shown in the structural complexity of the frontoclypeal region among females of *Proceratium*, and this variation is closely paralleled in the available males, each being similar to conspecific females. Moreover, the more extreme "proceratiine" head structure of *Discothyrea* females is also reflected in their males. Thus, it is not too surprising to find that the frontoclypeal structure of the *Probolomyrmex* male is similar to that of the females, and the similarities between the *Probolomyrmex* and *Discothyrea* males need in no way weaken Brown's argument. The palpal formula and wing venation are no more valuable as phylogenetic markers than in the female castes, and the genitalia are quite unspecialised, conforming to a basic ponerine plan. Similar simple genitalia occur in at least some males of *Proceratium*, *Discothyrea* and *Platythreia*, as well as in those of other genera.

The *Probolomyrmex* male differs from those of *Platythreia* in the characters discussed above and in the following additional features: it has single pectinate spurs on the middle and hind tibiae, and it lacks cerci, a terminal pygidial spine and an anal lobe on the hind wing. These same characters occur in males of *Proceratium* and *Discothyrea* as well as in those of many other ponerine genera; all are probably correlated with the small size of these animals and do not provide good phylogenetic markers. The lack of a median tooth on the pretarsal claws of all castes of *Probolomyrmex* need not preclude a platythyreine ancestor, since these structures occur in many ants as secondary adaptations to epigaeic foraging behaviour.

Ant larvae are very plastic organisms and may exhibit extreme modifications in response to specialised needs. Because of this, it is often difficult to evaluate the phylogenetic significance of their characters. *Probolomyrmex* larvae are extremely specialised, and very perplexing in this regard. The body form is unique among ponerines, and is no doubt correlated with the peculiar method by which the larvae are suspended from the ceiling of the nest by their terminal abdominal tubercles. The mandibles are rather ordinary but at least do not resemble those of *Proceratium* (G. C. and J. Wheeler, 1963, fig. 18, IIIa). The absence of papillae on the maxillary

and labial palps is known elsewhere in only one other ponerine genus, *Onychomyrmex* (tribe Amblyoponini) (G. C. and J. Wheeler, 1959, p. 638); this is almost certainly a convergently developed specialisation. A posteroventral tail is known only in two other Ponerine genera, *Platythyrea* and *Proceratium*! The low boss-like tubercles of *Probolomyrmex* larvae somewhat resemble those of *Proceratium*; however, similarly distributed, probably homologous, tubercles of diverse shape frequently occur in ponerine larvae (G. C. and J. Wheeler, 1952, 1964) so that the possibility of convergence in this character is very likely. *Platythyrea* larvae have a series of paired protuberances on the ventral side of the body. These appear to be homologous with the mid-ventral series of tubercles in *Probolomyrmex* and other ponerines; they may possibly indicate that the ancestral platythyreine larva was more generally tuberculate. The finely spinulose and papilligerous cuticle of the *Probolomyrmex* larva resembles that of *Platythyrea*, but similar cuticular structure occurs elsewhere in the Ponerinae and this resemblance could be convergent.

Although considerable information on the characters of *Probolomyrmex* is now available, a decision on the taxonomic position and phylogenetic affinities of the genus must still be largely subjective, dependent on the bias involved in "weighting" the various characters that could possibly represent phylogenetic indicators. Like Brown, I favour a platythyreine relationship for the genus, thus giving less weight to the characters of its "proceratiine habitus" than to the similarities with *Platythyrea*.

III. MEASUREMENTS AND INDICES

In a genus as structurally reduced as *Probolomyrmex*, the use of detailed measurements and indices calculated from them is essential in providing objective characterisation of the various species. All measurements cited in this paper were made with a stereomicroscope fitted with an ocular scale reading in units of 0.1 and 0.01 mm. directly, at a magnification of 100 \times . The various measurements and indices are defined as follows:—

Head length (HL): maximum mid-line length of head in full-face view, from median occipital border to clypeal apex.

Head width (HW): maximum width of head in full-face view, excluding eyes in the female castes, but including them in the male.

Scape length (SL): maximum measurable length of scape, not including its articular boss and condyle.

Cephalic index (CI): $HW \times 100/HL$.

Scape index (SI): $SL \times 100/HW$.

Weber's length of mesosoma (WL): diagonal length of mesosoma in lateral view, from the anterodorsal pronotal margin (i.e., point where pronotum joins cervix) to the posteroventral apex of the inferior lobe or flange on either side of the propodeal declivity.

Pronotal width (PW) (workers only): maximum width of pronotum viewed from directly above.

Mesonotal width (queens only): maximum width of mesoscutum viewed from directly above.

Dorsal petiole width: maximum width of petiolar node viewed from directly above.

Petiolar node index (workers only): dorsal petiole width $\times 100/PW$.

Petiole height: maximum height of petiolar segment in side view, measured vertically from the posteroventral corner of the subpetiolar process to the level of the petiolar apex.

Petiolar node length: maximum length of the node, measured longitudinally from the level of the spiracular process to that of the posteriormost extension of the petiolar tergum, where it surrounds the gastric articulation.

Lateral petiolar index: petiolar node length $\times 100$ /petiole height.

IV. KEY TO THE WORLD SPECIES OF *Probolomyrmex*

The following key is based exclusively on the worker caste and does not consider queens or males, since so few are known. The South American species *boliviensis* Mann, known only from the queen, is omitted.

- 1 Compound eyes present in only known specimen (figs. 13 and 14). *N.E. Africa* *brevirostris* (Forel) (p. 355)
 - Eyes completely lacking 2
- 2 Larger species (HL > 0.76 mm., WL > 1 mm.) 3
 - Smaller species (HL < 0.61 mm., WL < 0.88 mm.) 4
- 3 Head very narrow (CI, 58-59); scapes relatively very long (SI, 135-140); petiolar node in side view much longer than high (lateral petiolar index, 132-42); frons subopaque with distinct shagreening and overlying coarse puncturation. *Panama* *angusticeps* M. R. Smith (p. 360)
 - Head of unique holotype broader (CI, 63); scapes less elongate (SI, 113); petiolar node slightly higher than long (lateral petiolar index, 87-90); frons moderately shining, very finely shagreened with the puncturation almost effaced. *South Africa*. *filiformis* Mayr (p. 353)
- 4 Petiolar node distinctly longer than high in side view (lateral petiolar index, 115-120); scapes relatively long (SI, 100-103). *Java*; *Negros*, *Philippines* *dammermani* Wheeler (p. 356)
 - Petiolar node higher than long (lateral petiolar index < 93); scapes proportionately shorter (SI < 97) 5
- 5 Petiolar node considerably higher than long (lateral petiolar index 71) (distinguished from the sole remaining African species, *P. guineensis*, by much smaller size; HL, 0.51 mm. WL, 0.59 mm., against 0.61 and 0.80 mm. in *guineensis*). *N.E. Africa*. *brevirostris* (Forel) (p. 355)
 - Petiolar node relatively less high in side view (lateral petiolar index > 82). 6
- 6 Petiolar node with its posterior border almost straight when viewed from the side or above (fig. 23), the whole structure relatively broad in dorsal view (petiolar node index, 66-71). *E. Australia* *greavesi* sp. n. (p. 358)
 - Petiolar node with its posterior border distinctly concave in lateral view (figs. 12, 21, 35); node narrower in dorsal view (petiolar node index < 57) 7
- 7 Small Neotropical species (HL, 0.51 mm.; WL, 0.65 mm.), with relatively broad head (CI, 71) and very short scapes (SI, 81). *Panama* *petiolatus* Weber (p. 363)
 - Larger Old World species (HL, 0.59-0.61 mm.; WL, 0.79-0.80 mm.), with narrower heads (CI, 64-67) and considerably longer scapes (SI, 93-97). 8
- 8 Petiolar node in side view almost as long as high (lateral petiolar index, 93); subpetiolar process fairly low, moderately concave beneath (fig. 21). *Guadalcanal*, *Solomon Islands* *salomonis* sp. n. (p. 358)
 - Petiolar node shorter (lateral petiolar index, 84); subpetiolar process higher, its lower edge less concave in side view (fig. 12). *Guinea*; *W. Africa* *guineensis* sp. n. (p. 353)

V. DESCRIPTIONS AND RECORDS OF THE SPECIES

(1) *The African Species*

The three known Ethiopian species of *Probolomyrmex* are: *brevirostris* (Forel) (Northeast), *filiformis* Mayr (South) and *guineensis* sp. n. (West). The two last are similar and probably cognate, but *brevirostris* is very different from them. It is perhaps the most distinctive member of the genus, being the only known species in which eyes are developed in the worker caste. *P. brevisrostris* is further distinguished

from its African congeners by its small size and much shorter petiolar node. *P. filiformis* and *P. guineensis* differ in size, proportions and sculptural characters, as detailed below.

Probolomyrmex filiformis Mayr (figs. 8–10)

Probolomyrmex filiformis Mayr, 1901, *Ann. naturh. Hofmus. Wien* 16 : 3, ♀. Type locality: Port Elizabeth, South Africa.

Probolomyrmex filiformis: Arnold, 1915, *Ann. S. Afr. Mus.* 14 : 34, ♀. Redescription (of syntype?).

This is the type species of its genus, by monotypy. I have examined two syntype workers from the Mayr collection (Naturhistorisches Museum, Vienna); one is undamaged but the other lacks the head and gaster. These individuals are here selected as lectotype and paralectotype respectively and have been labelled accordingly.

Additional description. The aforementioned specimens have the following dimensions (lectotype cited first); HL, 0.76 mm.; HW, 0.48 mm.; SL, 0.54 mm.; CI, 63; SI, 113; WL, 1.03, 1.01 mm.; PW, 0.35, 0.37 mm.; dorsal petiole width, 0.23, 0.24 mm.; petiolar node index, 66, 65; petiole height, 0.39, 0.39 mm.; petiolar node length, 0.34, 0.35 mm.; lateral petiolar index, 87, 90. The descriptions of Mayr and Arnold adequately cover the general features of *P. filiformis*, which are illustrated in figures 8–10. As the subpetiolar process of the lectotype is damaged, that of the paralectotype is shown in figure 9; the posteroventral tooth of the process was present also in the specimen described by Arnold. The carina enclosing the posterior face of the node has its edge very feebly emarginate at the dorsal mid-line. When viewed from above, the declivitous face of the propodeum is moderately concave, the depth of the concavity being about one-eighth the distance between the dorsalmost corners of the posterolateral propodeal lamellae.

Details of sculpturation, required for comparison with the related *P. guineensis*, as follows: the 2 general sculptural elements, fine shagreening and associated coarse punctures, are present, but the puncturation is relatively weak. Entire surface of body, including mandibles, antennae and legs, very finely shagreened and moderately shining. Front and sides of head, entire pronotum and dorsum of mesosoma with very indistinct vestigial traces of overlying puncturation. Individual punctures increasingly distinct towards lower parts of sides of mesosoma; best developed, though still somewhat indistinct, on the mes- and metepisterna. Puncturation of sides of petiole similarly developed, that of first two gastric segments slightly less so.

Pilosity normal for the genus. Whitish, extremely fine, adpressed pubescence moderately well developed over entire body, most abundant on gaster and least so on dorsum of mesosoma and underside of head. The visible apical segments of maxillary and labial palpi, and the preapical maxillary segment, proportioned as in *P. angusticeps*.

Distribution.—Known only from the type locality, SOUTH AFRICA: Port Elizabeth (Brauns).

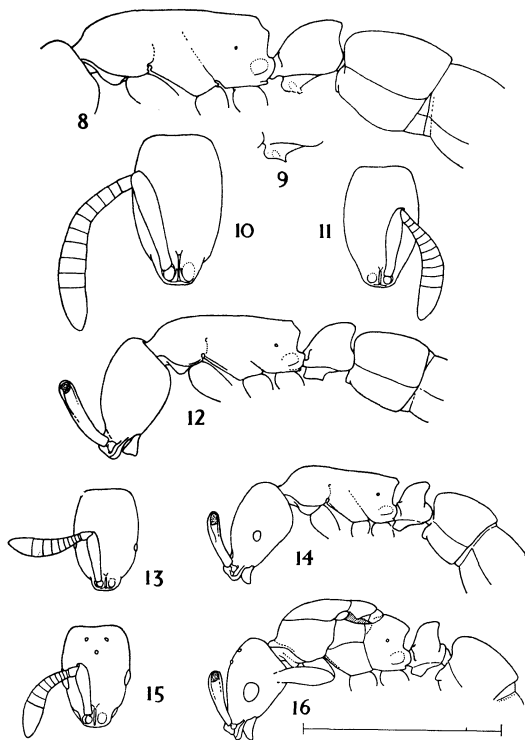
Probolomyrmex guineensis sp. n. (figs. 11, 12)

A series of *Probolomyrmex* from Guinea, originally housed in the Santschi collection but subsequently distributed, has been mentioned several times in the literature under the name *filiformis* Mayr, following Santschi (1914). I have retrieved three specimens of the original seven in this series and find them to be representative of a new species, here described.

Holotype worker

HL, 0.61 mm.; HW, 0.41 mm.; SL, 0.38 mm.; CI, 67; SI, 93; WL, 80.0 mm.; PW, 0.30 mm.; dorsal petiole width, 0.17 mm.; petiolar node index, 57; petiole height, 0.31 mm.; petiolar node length, 0.25 mm.; lateral petiolar index, 84. General features are shown in the figures. Close to *P. filiformis*, but differing from it in the following characters: (1) Smaller size, with relatively broad head, short scapes, and narrow, shorter petiolar node—as indicated in the above dimensions. (2) Punctural element of sculpturation more distinct (shagreening developed on all body and appendage surfaces, as in *filiformis*). Head capsule with moderately distinct superficial punctures, about 0.005 mm. in diameter, separated by distances about equal to their average diameter; those on sides and postgenal

areas most distinct. Punctuation of entire pronotum and remaining mesosomal dorsum similar to frons; punctures of mes- and metepisterna larger and more distinct. Petiole and first 2 segments of gaster with larger shallow punctures, about 0.01 mm. in diameter, separated by distances averaging about half this value. (3) Concavity of declivitous propodeal face, viewed from above, about one-quarter as deep as distance separating dorsal points of propodeal lamellae. (4) Subpetiolar process



Figs. 8-16.—African species of *Probolomyrmex*. (8-10) *P. filiformis* Mayr: (8) lectotype worker, mesosoma and petiole; (9) paralectotype worker, subpetiolar process; (10) lectotype worker, head. (11, 12) *P. guineensis* sp. n., holotype worker: (11) head; (12) body, side view. (13, 14) *P. brevirostris* (Forel), holotype worker: (13) head; (14) body, side view. (15, 16) *P. parvus* Weber, holotype queen: (15) head; (16) body, side view. Scale line equals 1.0 mm.

lacking an acute posteroventral tooth. When viewed from above, no trace of a median emargination of the posterior flange of the node.

P. guineensis resembles *filiformis* in all other respects, apart from slightly paler coloration. The three apical maxillary and the terminal labial palpal segments are proportioned as in *P. angusticeps*.

Paratype workers

Two paratype workers agree with the holotype in all essential characters, including details of the measurements and indices.

Holotype ♀ and 2 ♀ paratypes, GUINEA: Nigorie, Kakoulima (*Silvestri*). The holotype is deposited in the Naturhistorisches Museum, Basel, paratypes in the British Museum (Nat. Hist.) and the Muséum d'Histoire Naturelle, Geneva. There are differences in the original labels on these specimens. That of the holotype reads: Nigorie, Kakoulima (*Silvestri*); the Geneva Museum specimen has: Kakoulima 12 Ag. 1912; and the British Museum one has: French Guinea—d. F. Santschi—G. A. (presumably G. Arnold)—1914.

Probolomyrmex breviostris (Forel), **comb. n.** (figs. 13–16)

Escherichia breviostris Forel, 1910, *Zool. Jahrb. Syst.* 29: 246–7, ♀. Type locality: Ghinda, Eritrea. Holotype: Forel coll., Muséum d'Histoire Naturelle, Geneva (examined).

Synonymy.—A direct comparison of the holotype with that of *Probolomyrmex parvus* Weber (1949, *Amer. Mus. Nov.* 1398: 3, fig. 2, ♀; type locality: Busnia, Uganda; holotype: American Museum of Natural History) leaves little doubt that *parvus* is a synonym; the question is discussed below, and only the difference in caste between the two holotypes prevents a formal establishment of synonymy.

Holotype worker

HL, 0.51 mm.; HW, 0.34 mm.; SL, 0.27 mm.; CI, 67; SI, 79; WL, 0.59 mm.; PW, 0.25 mm.; dorsal petiole width, 0.15 mm.; petiolar node index, 60; petiole height, 0.28 mm.; petiolar node length, 0.20 mm.; lateral petiolar index, 71. General features as in figures 13 and 14 and in the original description.

This species is apparently unique in *Probolomyrmex* in the possession of well developed compound eyes in the worker. Those of the holotype are about 0.05 mm. in maximum diameter, with about 14 facets. Their anteriormost points are situated approximately 2.3 times their maximum diameter from the lateral base of the fronto-clypeal shelf. It is possible that the holotype is not normal for this character, for it could be a worker-queen intermediate. There is no compelling reason to assume this, however, and the specimen is provisionally accepted as a typical worker. In any case the synonymy of *parvus* and the distinctiveness of this species in *Probolomyrmex* would not be jeopardised if the worker was found to be normally eyeless, and such a discovery could only support the synonymy of *Escherichia* under *Probolomyrmex*.

The entire body is moderately finely shagreened and there is no trace of an accompanying coarse puncturation. Pilosity and pubescence as in *filiformis*.

Queen

(Based on the holotype of *parvus*, a dealated specimen.) HL, 0.50 mm.; HW (behind eyes), 0.35 mm.; SL, 0.27 mm.; CI, 70; SI, 77; WL, 0.67 mm.; mesonotal width, 0.28 mm.; dorsal petiole width, 0.16 mm.; petiole height, 0.26 mm.; petiolar node length, 0.19 mm.; lateral petiolar index, 73. General features as in figures 15 and 16. Differing from the worker in the usual characters. Maximum diameter of compound eyes, 0.11 mm. Form of head, mandibles and petiolar node almost exactly as in worker. Mesosomal structure complete. Sculpturation, pilosity and pubescence developed similarly to those in worker; ground colour slightly darker reddish-brown, eyes dark brown, almost black, each ocellus with an adjacent dark brown spot, suture lines of mesosoma infuscated.

The oral palpi are not visible in the worker, but the general form of the three apical maxillary and the terminal labial palpomeres of the queen is normal for the genus. The terminal maxillary segment is about 5 times as long as broad.

Distribution.—Apparently widespread in North East Africa. ETHIOPIA: Eritrea, Ghinda (type locality of *brevirostris*); UGANDA: Busnia (*N. A. Weber*) (type locality of *parvus*).

Biology.—The holotype bears a label reading "bei termiten". *Weber's* queen was taken "among humus and leaves at the base of a tree with a few bushes forming an island in a banana plantation."

(2) *The Indo-Australian Species*

The three species of *Probolomyrmex* known from the Indo-Australian area are all closely related and probably cognate. *P. dammermani* Wheeler (Java and Negros, Philippines) and *P. salomonis* sp. n. (Guadalcanal, Solomon Islands) are fairly similar, whereas the eastern Australian *P. greavesi* sp. n. is more distinctive. Further species of *Probolomyrmex* will almost certainly be found to occur on the islands of Indonesia and Melanesia, especially on New Guinea. The genus is likely to be present also on the south-east Asian mainland.

Probolomyrmex dammermani Wheeler (figs. 17-19)

Probolomyrmex dammermani Wheeler, 1928, *Psyche*, Camb., Mass. 35 : 7-9, fig. 1, ♀. Type locality: Buitenzorg, Java.

Additional description

The following notes are based on a single syntype worker (labelled "cotype") in the Museum of Comparative Zoology (type No. 26427). The general accuracy of Wheeler's original description has been confirmed by study of this specimen, but a few additions and corrections are indicated.

(1) HL, 0.60 mm.; HW, 0.41 mm.; SL, 0.42 mm.; CI, 68; SI, 103; WL, 0.81 mm.; PW, 0.33 mm.; dorsal petiole width, 0.19 mm.; petiolar node index, 58; petiolar height, 0.25 mm.; petiolar node length, 0.30 mm.; lateral petiolar index, 120.

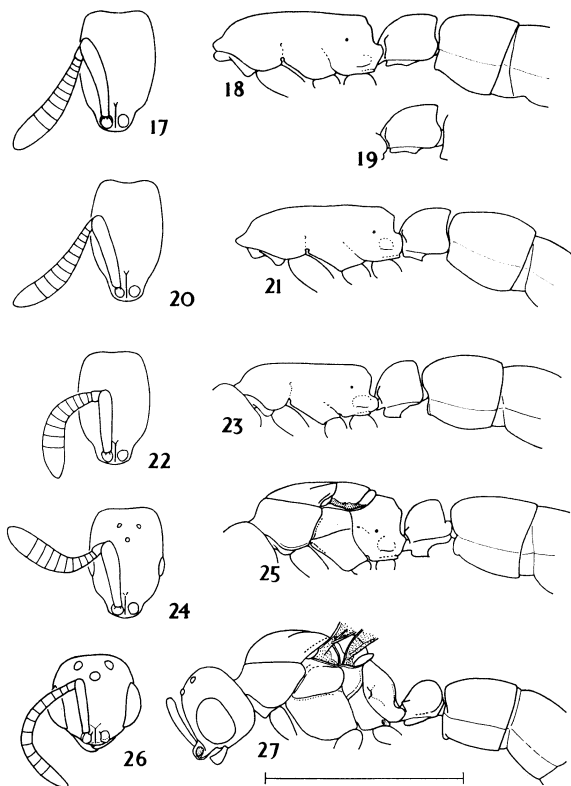
(2) First funicular segment of antenna about one-fifth longer than broad, and terminal segment one-quarter longer than the three preceding segments together.

(3) The two sculptural components normal for the genus present. Fine shagreening everywhere well developed, and overlying puncturation very distinct. Punctures of frons and dorsa of mesosoma, petiole and gaster about 0.01 mm. in diameter and spaced at about the same distance. Postgenal punctures, and those of sides of mesosoma and ventral and lateral aspects of petiole and gaster, larger, averaging about 0.02 mm. in diameter, and variously spaced, from intervals about equal to their maximum diameter to near contiguity.

(4) Mandibular dentition not visible, but apical two maxillary and terminal labial palpomeres with proportions similar to those of *P. angusticeps*.

Two additional worker specimens in the Museum of Comparative Zoology are apparently referable to *P. dammermani* and allow extension of its range to the Philippine Island of Negros. One of these is teneral, and was not measured; the other has the following dimensions: HL, 0.60 mm.; HW, 0.40 mm.; CI, 67; WL, 0.88 mm.; PW, 0.31 mm.; dorsal petiole width, 0.17 mm.; petiolar node index, 55; petiole height, 0.26 mm.; petiolar node length, 0.30 mm.; lateral petiolar index, 115. This specimen has lost its antennae, but the other has a scape index of about 100. The mandibular dentition consists of a single large apical tooth followed by a smaller pre-apical one and five small denticles. The palpal formula is maxillary 4: labial 2 (teneral dissected), with the segmental proportions as in *P. angusticeps*.

These specimens are very similar to the Javanese syntype in size, general form, sculpturation, pilosity and pubescence. The following slight differences from the syntype are noted: (1) the occipital border is somewhat less concave; (2) the posterior part of the subpetiolar process is more expanded (*cf.* figs. 18 and 19); (3) the colour, even that of the less teneral specimen, is a much lighter yellowish-brown; this is almost certainly due, however, to that specimen being partly callow.



FIGS. 17-27.—Indo-Australian species of *Probolomyrmex*. (17-18) *P. dammermani* Wheeler, cotype worker: (17) head; (18) body, side view. (19) *P. dammermani*, specimen from Negros, Philippines, petiolar node, side view. (20, 21) *P. salomonis* sp. n., holotype worker: (20) head; (21) body, side view. (22, 23) *P. greavesi* sp. n., holotype worker: (22) head; (23) body, side view. (24, 25) *P. greavesi*, paratype queen: (24) head; (25) body, side view. (26, 27) *P. greavesi*, paratype male: (26) head; (27) body, side view. Scale line equals 1.0 mm.

Distribution.—*P. dammermani* is known from only the two collections discussed above. INDONESIA: Java, Buitenzorg (type locality), 12.xii.1922 (*Dammerman*); PHILIPPINE ISLANDS: Negros, Dumaguete, 16.iv.1931 (*J. W. Chapman*).

Relationships.—*P. dammermani* is closely related to the other Indo-Australian species, *P. salomonis* and *P. greavesi*. It is distinguished from them by the proportions of the node and the shape of its subpetiolar process. *P. salomonis* has a proportionately narrow head, and the antennal scapes of *greavesi* are somewhat shorter.

***Probolomyrmex salomonis* sp. n. (figs. 20, 21)**

Holotype worker

HL, 0.59 mm.; HW, 0.38 mm.; SL, 0.37 mm.; CI, 64; SI, 97; WL, 0.79 mm.; PW, 0.30 mm.; dorsal petiole width, 0.17 mm.; petiolar node index, 57; petiolar height, 0.28 mm.; petiolar node length, 0.26 mm.; lateral petiolar index, 93. General form as shown in the figures. Habitus similar to that of *P. dammermani* and *P. greavesi*. Head narrower than in these species, with occipital border moderately concave. Scape relatively as long as in *dammermani*, somewhat longer than in *greavesi*. Eyeless. Mandible with a large acute apical tooth followed by a series of six denticles, distal one of which slightly enlarged. Visible terminal maxillary and labial palpomeres proportioned as in *P. angusticeps*. General form of mesosoma as in *P. dammermani*. Declivitous face of propodeum, viewed from above, moderately concave, depth of concavity about one-third distance between dorsal corners of posterolateral propodeal lamellae. Petiolar node as in figure 21; posterior face moderately concave in side view, its surrounding flange feebly emarginate at dorsal mid-line. Subpetiolar process well developed, similar to that of *P. greavesi*, but shallower and with ventral edge distinctly concave in side view.

Pilosity reduced, as is normal for the genus; pubescence extremely fine and very sparse, most abundant on second segment of gaster, virtually lacking on head, mesosoma and node. Sculpturation almost exactly as described above for *P. dammermani*. Colour rich golden-brown, as in the type of *P. dammermani*.

Holotype ♂, SOLOMON ISLANDS: Guadalcanal, Mt. Austen, Honiara, 25.ii.1963 (*P. J. M. Greenslade*). The unique holotype is deposited in the Museum of Comparative Zoology, Harvard University.

Distribution.—Known only from type locality.

Biology.—The holotype was collected in a Berlese funnel sample of leafmould from the floor of undisturbed rainforest, at an elevation of about 1000 feet.

Relationships.—This species is clearly close to *P. dammermani*, and is distinguished from it mainly by the shorter petiolar node (lateral petiole index 93, compared with 115–120 in *dammermani*), with a much more distinct subpetiolar process. The Australian *P. greavesi* is also related, but it has an even shorter petiolar node (lateral petiolar index 82–83), which is thicker in dorsal view (petiolar node index 66–69, opposed to 57 in *salomonis*), and somewhat shorter antennal scapes (SI 85–87, compared with 97 in *salomonis* and 103 in *dammermani*). *P. salomonis* bears a general resemblance to the east African *P. guineensis*, but the two differ in proportions, especially those of the petiolar node, and in the intensity of sculpturation.

***Probolomyrmex greavesi* sp. n. (figs. 2, 22–27)**

Holotype worker

HL, 0.56 mm.; HW, 0.39 mm.; SL, 0.34 mm.; CI, 70; SI, 87; WL, 0.71 mm.; PW, 0.28 mm.; dorsal petiole width, 0.20 mm.; petiolar node index, 71; petiole height, 0.29 mm.; petiolar node length, 0.24 mm.; lateral petiolar index, 83. General features as shown in figures 22 and 23. Habitus similar to the related species *dammermani* and *salomonis*. Cephalic proportions as in *dammermani*, occipital border almost straight, and sides of head slightly more convex. Eyeless. Scape somewhat shorter than in either of the above species; basal funicular segment about one-third longer than broad, segments 2–10 broader than long, second subequal in length to third; apical segment slightly longer than the three preceding together. Mandible with an acute apical tooth followed by a series of seven or eight small denticles, anterior one of which is very slightly enlarged.

Mesosoma as in *P. dammermani*. Petiolar node shorter than in either *dammermani* or *salomonis*, its posterior border almost perfectly straight when viewed from side or from above. Subpetiolar process well developed, subrectangular; its anteroventral angle narrowly rounded, posteroventral one produced as a small posteriorly directed tooth; lower edge feebly concave, almost straight.

Subopaque, sculpturation as in *P. dammermani*, punctural component somewhat less distinctly incised, almost lacking on mesosomal dorsum. Pubescence and pilosity as in *dammermani*.

Body medium-light golden-brown; antennae, legs and apex of gaster a shade lighter.

Paratype workers

Three paratype workers, from same nest series as holotype, have the following dimensions: HL, 0.56–0.58 mm.; HW, 0.39 mm.; SL, 0.33–0.34 mm.; CI, 67–70; SI, 85–87; WL, 0.73–0.76 mm.; PW, 0.29 mm.; dorsal petiole width, 0.19–0.20 mm.; petiolar node index, 66–69; petiole height, 0.30 mm.; petiolar node length, 0.25 mm.; lateral petiolar index, 83. Palpal formula, maxillary 4: labial 2 (dissected), general proportions of palp segments as in *P. angusticeps*. No significant structural variation shown among these specimens.

Two additional paratype workers from Greenmount, south Queensland, are smaller than those from type nest, but resemble them in all apparently significant characters: HL, 0.52, 0.55 mm.; HW, 0.36, 0.37 mm.; SL, 0.31, 0.32 mm.; CI, 69, 67; SI, 86, 86; WL, 0.66, 0.68 mm.; PW, 0.27, 0.27 mm.; dorsal petiole width, 0.17, 0.18 mm.; petiolar node index, 67, 67; petiole height, 0.27, 0.28 mm.; petiolar node length, 0.22, 0.23 mm.; lateral petiolar index, 82, 82.

Paratype queens (figs. 2, 24, 25)

Four queens present in type nest series: a rather worn, large headless specimen (probably the colony mother-queen), two winged ones and a little-worn dealate (all apparently virgins). These specimens have the following dimensions (those of the headless specimen cited last where applicable). HL, 0.54–0.56 mm., HW (behind eyes), 0.38–0.40 mm.; SL, 0.33 mm.; CI, 69–71; SI, 83–87; WL, 0.74–0.75 mm., 0.77 mm.; mesonotal width, 0.29, 0.30 mm.; dorsal petiole width, 0.17–0.18 mm., 0.20 mm.; petiole height, 0.27–0.28 mm., 0.30 mm.; petiolar node length, 0.20–0.22 mm., 0.24 mm.; lateral petiolar index, 74–79, 77. Differing from worker in the usual characters. Maximum diameter of compound eye 0.11 mm., ocelli small. Details of antennal, mandibular and palpal structure as in worker. Mesosoma structurally complete. Form of petiole and gaster as in worker. Wing venation as in figure 2, similar to that of *P. angusticeps*.

Sculpture, pubescence, pilosity and colour of body and appendages as in worker; eyes black, each ocellus with an adjacent black spot, mesosomal suture lines faintly infuscated, wings clear, their veins pale yellow, pterostigma pale brown.

Paratype male

A single specimen from the *greavesi* type nest series is the only known male of *Probolomyrmex*.

HL, 0.47 mm.; HW (across eyes), 0.49 mm.; SL, 0.38 mm.; WL, 0.84 mm.; mesonotal width, 0.39 mm.; dorsal petiole width, 0.14 mm.; petiole height, 0.18 mm.; petiolar node length, 0.22 mm. General characters as discussed in the generic diagnosis above and shown in figures 26 and 27. Compound eyes large, finely faceted, their maximum diameter 0.23 mm. Ocelli very large, their average diameter about 0.05 mm. Palpal segmentation, maxillary 4: labial 2 (dissected), proportions of palpmere almost exactly as in worker. Basal and declivitous faces of propodeum forming an even curvature in side view; declivitous face very slightly concave in dorsal view, with weak, obtuse posterolateral lamellae. Propodeal spiracle directed posteriorly, area behind it slightly concave.

Mandibles antennae and frontoclypeal process finely punctate. Head and mesosomal dorsum subopaque, fairly coarsely shagreened. Sides of mesosoma more lucid, with fairly close, fine puncturation, which is almost effaced on parts of mesanepisternum. Declivitous face of propodeum smooth and shining. Petiole and gaster subopaque and indistinctly sculptured with a partly effaced, dense, medium puncturation, which is finer on node than gaster.

Colour dull dark reddish-brown. Mandibles, antennae, legs and terminalia yellowish-brown. Eyes black. Wing veins light yellowish-brown; pterostigma slightly darker.

Holotype ♀, AUSTRALIA: Australian Capital Territory, Mt. Stromlo (type locality), 11.iii.1933 (*T. Greaves*). **Paratypes**: 3 ♀, 4 ♂, 1 ♂, same data as type; 2 ♀, Queensland, Greenmount, 4.xii.1949 (*T. Greaves*).

The holotype, paratype male, and most paratype workers and queens are deposited in the Australian National Insect Collection, C.S.I.R.O., Canberra. Other paratypes are in the Museum of Comparative Zoology (1 ♀, 1 ♂) and the National Museum of Victoria, Melbourne (1 ♀).

Ecology.—The Mt. Stromlo material was collected under rocks in pine litter in a plantation of exotic *Pinus radiata*. The Greenmount material was taken in open *Eucalyptus* woodland, on a hill overlooking treeless downs. According to Mr. Greaves they were probably collected under a rock.

Relationships.—Close to *P. dammermani* and *P. salomonis*, but differing from them

in the form of the petiolar node and the relative proportions of the head and antennal scapes (see above under *P. salomonis*).

(3) *The Neotropical Species*

Three species of *Probolomyrmex* are known from the Neotropical Region. Two of them, *P. angusticeps* Smith and *P. petiolatus* Weber, are sympatric on Barro Colorado Island, Panama, whereas the third species, *P. boliviensis* Mann, is from Bolivia. The two latter species are represented only by the holotypes, a worker and a queen respectively, but the worker types of *angusticeps* have recently been supplemented by further material from the type locality; this includes alate and dealate queens, larvae and pupae. *P. petiolatus* is the most distinctive of these species. *P. angusticeps* and *P. boliviensis* are rather alike and probably closely related; they could conceivably be geographical variants of a single species.

Probolomyrmex angusticeps M. R. Smith (figs. 1, 3-7, 28-31)

Probolomyrmex angusticeps M. R. Smith, 1949, *Proc. ent. Soc. Wash.* 51: 39, ♀. Type locality: Barro Colorado Island, Panama Canal Zone.

The following notes are based on a series of ten workers and five queens from a colony collected by the author on June 21st, 1961, at the type locality, Barro Colorado Island. I have not seen the holotype or paratype of *P. angusticeps*, but workers from the material discussed here have been determined by comparison with them, by Dr. M. R. Smith.

Worker (figs. 28, 29)

The following characters are given additional to those stated in Smith's original description.

(1) Dimensions (N = 10): HL, 0.76-0.80 mm.; HW, 0.45-0.47 mm.; SL, 0.61-0.64 mm.; CI, 58-59; SI, 135-140; WL, 1.12-1.17 mm.; PW, 0.39-0.41 mm.; dorsal petiole width, 0.22-0.24 mm.; petiolar node index, 56-62; petiole height, 0.31-0.34 mm.; petiolar node length, 0.44-0.46 mm.; lateral petiolar index, 132-142.

(2) Palpal formula, maxillary 4: labial 2 (4 specimens dissected). Proportions of the palp segments vary slightly; typically the three basalmost approximately subequal in length, and about 1.5 times as long as broad; apical segment slightly narrower and about 3 times as long as broad; in some instances second segment elongated to almost 2.5 times its breadth; labial palp segments narrow and relatively elongate, basal having about same proportions as apical maxillary segment, and apical about 4 times as long as broad, and 1.25 times as long as basal segment.

Workers very uniform in structure, but showing slight variation in shape of subpetiolar process.

Queen (figs. 1, 30, 31)

The five queens mentioned above have the following dimensions: HL, 0.74-0.76 mm.; HW (behind eyes), 0.46-0.47 mm.; SL, 0.60-0.62 mm.; CI, 61-63; SI, 130-132; WL, 1.13-1.18 mm.; mesonotal width, 0.40-0.42 mm.; dorsal petiole width, 0.23-0.24 mm.; petiole height, 0.33-0.35 mm.; petiolar node length, 0.43-0.45 mm.; lateral petiolar index, 128-130; palpal formula, maxillary 4: labial 2 (2 specimens dissected). These specimens differ from the workers in the usual characters of full sexuality discussed in the generic diagnosis above. Colour generally as in worker (medium reddish-brown), eyes blackish-brown, each ocellus with an associated dark brown spot. Wing venation (fig. 1) similar to that of *P. greavesi*. Palpal structure identical to that of workers. Characters differentiating these specimens from the queen of the related *P. boliviensis* are given below.

The larval characters of *P. angusticeps* are discussed above (p. 348, figs. 3-7). The pupae are peculiar for ponerines in lacking cocoons.

Distribution.—Known only from the type locality, PANAMA: Barro Colorado Island.

Biology.—My Barro Colorado accession originally consisted of 22 workers, 7 queens (4 alate), 11 pupae (9 worker, 2 male), 2 pharate pupae and 6 larvae of various instars. These were collected from an old beetle gallery in a fairly sound, dry portion of a rotting branch about 30 cm. long and 8-10 cm. in diameter, lying on the floor of primary rainforest. The ants were in a single group occupying almost 3 cm. of the

gallery, which was about 6–10 mm. in diameter. An aspirator device was used for collection, and it is presumed that the whole colony, excluding foragers, was taken. One of the queens was more worn than the others and appeared to be the "mother-queen" of the colony. The specimens were immediately placed in a glass-topped plaster-of-Paris observation cell, in which they survived for six days until the death of the queen and the larvae disrupted their behaviour. A number of eggs were accumulated during this period, at least two of them being laid by the queen. One worker completed its development while under observation.

Various small soil arthropods including assorted Collembola, Symphyla, small immature spiders, larval and adult ants, Diptera, Coleoptera and termites at all stages of development, and various arthropod and other eggs collected from leafmould, were placed in the nest from time to time. None of these organisms were attacked or accepted as food; indeed, the ants usually retreated hurriedly with their brood when confronted by other animals.

The larvae and pharate pupae, still enclosed in larval cuticles, were not placed by the nurse workers on the nest floor, but were attached to the plaster walls or glass ceiling of the brood chamber by the peculiar terminal abdominal suspensory tubercles described above (p. 348), so as to hang head downwards. Eggs and pupae were normally placed on the floor of the brood chamber, but under moist conditions they too were attached to the nest ceiling, presumably being held there by the surface tension forces of the moisture film on the glass. Pupae were invariably placed with the frontal region of the head adherent to the ceiling, and the eggs were attached either directly to the ceiling, or to the bodies of larvae or pupae.

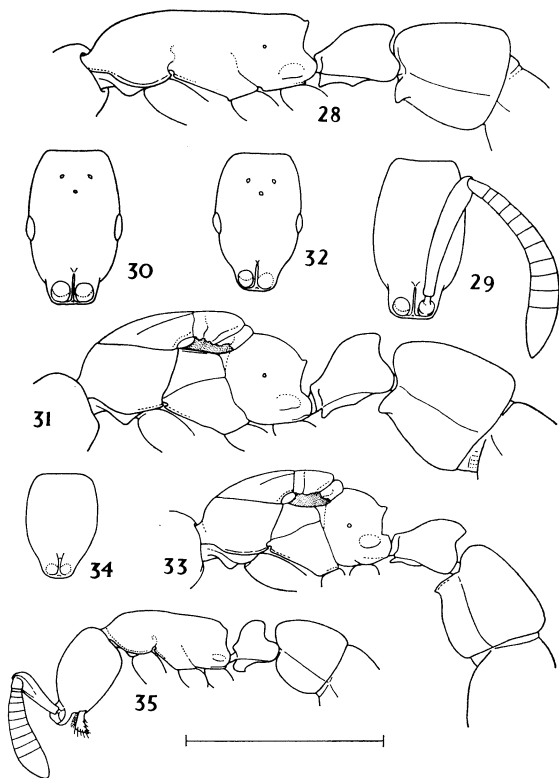
The workers were very active and "excitable", being reminiscent of *Leptogenys* or *Platythyrea* in this regard. They ran quite rapidly and "nervously" when disturbed and, even when settled, were constantly active, grooming themselves and their partners. The larvae were assiduously attended and were almost constantly being licked by one or more of the workers. The suspended brood was usually placed immediately above the main adult cluster, the nurse workers moving on to the ceiling to attend to the larvae.

Workers were not observed transporting their fellows, but the queen was carried about 5 cm. in the jaws of a worker on one occasion. She lay in a pupal posture and was held by the frontal part of the head, lying ventral side uppermost along the underside of the transporting worker. Pupae were always normally carried in this way, although they were sometimes dragged by the legs or antennae when being positioned by nurse workers. The larvae were always carried along the underside of transporting workers and were invariably gripped about the neck of the terminal abdominal suspensory tubercle. This mode of grasping the larvae appeared to facilitate their placement on the nest ceiling by the workers. The newly emerged workers are highly callow, and apparently take about 5 days to attain full coloration.

Probolomyrmex boliviensis Mann (figs. 32, 33)

Probolomyrmex boliviensis Mann, 1923, *Psyche, Camb., Mass.* 36 : 16, fig. 2, ♀. Type locality: Rurrenabaque, Bolivia. Holotype: United States National Museum (Type No. 25906) (examined).

Mann's unique holotype queen of *P. boliviensis* has the following dimensions: HL, 0.66 mm.; HW (behind eyes), 0.43 mm.; SL, 0.47 mm.; CI, 65; SI, 109; WL, 0.95 mm.; mesonotal width, 0.33 mm.; dorsal petiole width, 0.20 mm.; petiole height, 0.27 mm.; petiolar node length, 0.34 mm.; lateral petiolar index, 126. As perusal of the relevant figures will verify, *P. boliviensis* closely resembles the queen of the Panamanian *P. angusticeps*, and there is a possibility that these two forms are mere geographical variants of a single species. At present it does not seem advisable to upset their separate status, which can be clarified only by study of additional material.



FIGS. 28-35.—Neotropical species of *Probolomyrmex*. (28, 29) *P. angusticeps* M. R. Smith, worker: (28) body, side view; (29) head. (30, 31) *P. angusticeps*, queen: (30) head; (31) body, side view. (32, 33) *P. boliviensis*, holotype queen: (32) head; (33) body, side view. (34, 35) *P. petiolatus* Weber, holotype worker: (34) head; (35) body, side view. Scale line equals 1.0 mm.

The *boliviensis* holotype differs from her Panamanian counterparts in the following characters:

(1) Smaller size (HL, 0.66 mm. against 0.74–0.76 mm. in *angusticeps*), with relatively broad head (CI, 65 against 61–63) and node (petiolar node width, 0.61 times the mesonotum width against 0.55–0.57 times in *angusticeps*).

(2) Antennal scapes proportionately much shorter (SI, 109 as opposed to 130–132 in queens of *angusticeps*).

(3) Sculpturation similar in distribution and relative intensity on different parts of the body, but superficial punctures of head, mesosomal dorsum and node distinctly less clearly incised in *boliviensis*.

Mann reported the palpal formula as maxillary 3: labial 2. This observation was based on the undissected holotype, and only the visible segments were considered. After studying the specimen I believe that the true maxillary count is probably 4, as in other species of *Probolomyrmex*. The general proportions of the palpal segments are as described above for *P. angusticeps*.

Distribution.—Known only from the type locality, BOLIVIA: Rurrenabaque (*W. M. Mann*).

Biology.—The unique holotype was taken beneath a stone, near a small colony of *Ponera*.

Probolomyrmex petiolatus Weber (figs. 34, 35)

Probolomyrmex petiolatus Weber, 1940, *Psyche, Camb., Mass.* 47, 76, fig. 1, ♀. Type locality: Barro Colorado Island, Panama Canal Zone. Holotype: N. A. Weber Collection (examined).

The unique holotype worker of this species is illustrated in figures 34 and 35. It has the following dimensions: HL, 0.51 mm.; HW, 0.36 mm.; SL, 0.29 mm.; CI, 71; SI, 81; WL, 0.65 mm.; PW, 0.27 mm.; dorsal petiole width, 0.14 mm.; petiolar node index, 52; petiole height, 0.27 mm.; petiolar node length, 0.23 mm.; lateral petiolar index, 85. Weber's original description adequately characterises this distinctive species. The worker of *P. petiolatus* differs from that of the sympatric *P. angusticeps* in its smaller size, with relatively broad head, much shorter scapes, and shorter, more compact petiolar node. The unknown worker of *P. boliviensis* is undoubtedly similar to *P. angusticeps* in these features.

Distribution.—Known only from the type locality, PANAMA: Barro Colorado Island.

Ecology.—The holotype was collected among leaves and humus on the rainforest floor.

VI. A SPECIES PROPERLY EXCLUDED FROM *Probolomyrmex*: (?) *Leptanilla palauensis*
(M. R. Smith), **comb. n.**

Probolomyrmex palauensis M. R. Smith, 1953, *J. N.Y. ent. Soc.* 61: 127–129, figs. 1–2, ♂. Type locality: S.W. of Ulimang, Babelthau I., Palau Islands, Micronesia. Holotype: United States National Museum (examined).

This species was described from a single male collected without associated workers or queens. The general habitus is somewhat like that of the female castes of *Probolomyrmex*, but knowledge of the male of *P. greavesi* precludes the possibility that *palauensis* belongs in that genus.

A completely satisfactory generic assignment for *palauensis* is not possible at present. Inclusion in the Formicidae is acceptable on the basis of the nodal form and other general characters, although metapleural glands are not visible on the specimen. The presence of these organs is apparently a universal and definitive character in female ants, but their presence among the males has never been objectively surveyed. A spot check in the Museum of Comparative Zoology collection shows that metapleural glands are lacking, or externally indiscernible, in the males of many genera. Placement in the subfamily Ponerinae is not tenable, since all known ponerine ants, of all

castes, have the tergum and sternum of the second post-petiolar (fourth true abdominal) segment fused laterally to form a strong tubular structure and this is not so in the holotype of *palauensis*.

I have concluded that a queried assignment to the genus *Leptanilla* (subfamily Leptanillinae) provides the best placement for *palauensis*. A number of male-based species have been described in *Leptanilla* or in the possibly synonymous genus *Phaulomyrma* by Santschi (1907, 1908) and by G. C. & E. W. Wheeler (1930). However, none of the known leptanilline males were collected in definite association with workers, and until such specimens are available the status of the Wheeler and Santschi species must be questioned. The only presumed leptanilline male available here for comparison with *palauensis* is the holotype of *Phaulomyrma javana* Wheeler and Wheeler. The two specimens agree sufficiently well for relationship between them to be reasonably assumed: if *Phaulomyrma* is truly a leptanilline ant, then *palauensis* probably is also.

The holotype of *palauensis* resembles the presumed *Leptanilla-Phaulomyrma* males in the following features:

(1) The structure of the head, mandibles, frontoclypeal region, antennae, eyes and ocelli. The oral palpi are unfortunately not visible in *palauensis*.

(2) The torn wing fragments appear to have had extremely reduced venation, as in the leptanillines.

(3) The presence of one apical spur on the middle tibia and two on the posterior one, a feature characteristic of several of the described "*Leptanilla*" males.

(4) Fusion of the lateral mesosomal sclerites is more marked in *palauensis* than in the leptanillines, but the form of this tagma and of the petiole and gaster, is similar.

(5) The apparent absence of metapleural glands, which are not visible in the slide-mounted type of *Phaulomyrma*, even under phase-contrast examination.

(6) Workers and queens of available *Leptanilla* species do not have the sclerites of the fourth abdominal segment fused laterally. This is so in the *Phaulomyrma* male, and apparently also in the described *Leptanilla* males, as well as in the type of *palauensis*.

(7) The peculiar structure of the terminalia, especially that of the much enlarged non-retractile genital capsule, with its greatly elongated aedeagus. Wheeler & Wheeler (1930: fig. 2c) show a ventral view of the genital capsule of *Phaulomyrma*. In the specimen illustrated the apices of the gonoforceps are folded inwards in an apparently unnatural position; if they were unfolded the genital apex would closely resemble that of *palauensis*, as shown in Smith's figure 2. A similar folding of the gonoforceps evidently occurred in the specimens illustrated by Santschi, and with appropriate correction they too would resemble *palauensis*.

According to the diagnoses of Wheeler & Wheeler (1930), *palauensis* appears closer to *Phaulomyrma* in some features than to *Leptanilla*. However, placement of this species in *Leptanilla* seems sensible in view of the uncertainty surrounding the status of all these forms.

VII. SUMMARY

The world fauna of *Probolomyrmex* Mayr is reviewed. Nine species are recognised: three African, three Indo-Australian and three Neotropical. The genus *Escherichia* Forel is placed in synonymy under *Probolomyrmex*. The male described as *P. palauensis* M. R. Smith is provisionally transferred to the genus *Leptanilla*. Three new species are described: *P. greavesi* (Australia), *P. guineensis* (Guinea) and *P. salomonis* (Guadalcanal). The male, larva and pupa of the genus are described for the first time, as well as queens collected in definite association with their workers. A key to the species is presented and all known castes of all species are figured, mostly from type material. Biological observations on *P. angusticeps* M. R. Smith (Panama) are reported. The larvae and pharate pupae are suspended from the nest ceiling by a

peculiar median suspensory tubercle on the terminal segment of the larval abdomen. The pupae, which are naked (a rare character in subfamily Ponerinae), are also suspended, by the frontal regions of their heads, if a moisture film is present.

The research for this paper was supported by the United States National Science Foundation Grant No. GB 1634 "Classification and Population Biology of the Indo-Australian Ants". Field studies in 1961 on Barro Colorado Island, Panama Canal Zone, were supported by a grant from Sigma Xi-RESA. I wish to thank the following individuals and Museums for loan or donation of specimens: Dr. C. Besuchet (Muséum d'Histoire Naturelle, Geneva); Professor P. J. Darlington (Museum of Comparative Zoology, Cambridge, Mass, U.S.A.); Dr. M. Fischer (Naturhistorisches Museum, Vienna); Dr. P. J. M. Greenslade (Agriculture Department, British Solomon Islands); Dr. F. Keiser (Naturhistorisches Museum, Basel); Dr. K. H. L. Key and Mr. T. Greaves (Australian National Insect Collection, C.S.I.R.O., Canberra); Dr. J. G. Rozen, Jr., (American Museum of Natural History); Dr. M. R. Smith and Dr. K. V. Krombein (United States National Museum); Dr. N. A. Weber (Swarthmore College, Pennsylvania); and Drs. G. C. and J. Wheeler (University of North Dakota). Dr. Krombein and Dr. H. E. Evans have aided in discussing the problem of the assignment of *P. palauensis*.

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(Manuscript received 28th September, 1964)